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Postembryonic Development and Life Cycle of *Atypus karschi* DÖNITZ (Araneae: Atypidae)

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宮下和喜[1)]：ジグモの幼生（若虫）発育と生活環

Abstract Development and web growth of *Atypus karschi* were investigated by means of individual rearings under semi-outdoor conditions. Males required 3 years for development from egg to adulthood, passing through 8–9 molts after emerging from the maternal web. Females also developed to adults in 3–4 years with a variable post-emergent molt number from 9 to 11. The mean web width increased from 2.3 mm to 13.3 mm in males and 13.7 mm in females during the period of nymphal development. In the case of adult females, however, web width continued to grow up to 15.9 mm or more, since they lived for 3 or more years and repeated a post-adult molt every year. From the examination of seasonal change in weekly excretion frequencies through one year, it was observed that adults and nymphs were still active even in winter. The life cycle of this species is described based on these results and field observations.

Introduction

The purse-web spider *Atypus karschi* DÖNITZ is common in Japan (YAGINUMA, 1978). They live in a tubular web of which the upper half is constructed vertically and attached to some suitable stem or rock, while the lower half is under the ground. They usually live in shady and humid places such as woods and shrubberies, and seldom or never emerge from the web. Probably because of its secluded and inconspicuous life-style, this spider has rarely attracted arachnologists as a suitable subject for ecological investigation. The majority of works on *A. karschi*, most of which are cited by YOSHIKURA (1987), were fragmentary and sometimes contained unreliable descriptions. There has been no precise investigation of the development and growth of this spider, except for YOSHIKURA's (1958) study of postembryonic development to the 1st instar nymph.

In the present work, therefore, I investigated the nymphal development and web growth of *A. karschi* by means of individual rearings under semi-outdoor conditions from 1986 to 1991. Certain field observations and samplings were also conducted in parallel with the individual rearings, in order to obtain full knowledge of the life cycle.

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Materials and Methods

Individual rearings. The experimental animals were 1st instar nymphs obtained from one mother's web dug out in a field near the Chuo-gakuin High School in Abiko-shi, Chiba Prefecture, on 28 November 1986. Fifty-two nymphs were kept individually in plastic containers, 5.3 cm in diameter and 12.5 cm in height. A 5–6 cm layer of damp soil was placed in the bottom of each container, and the top was covered with a piece of cotton cloth. After one year, these containers were replaced by larger ones, 11.3 cm in diameter and 25.7 cm in height, with a 10–12 cm layer of damp soil. Rearings were conducted under semi-outdoor conditions protected from direct sunlight, rain and wind; thus temperature and humidity were not controlled. The maximum ambient temperature in summer ranged between 35.2° and 36.6°C, and the minimum temperature in winter between −3.8° and −5.2°C. A sufficient quantity of water was applied to the soil to keep it moist. The inside of the container was cleaned when it became filthy with excreta. The animals were given suitable prey at intervals of 3–4 days in 1986 and 1987, but thereafter every 5–7 days, extended to 7–10 days during the winter in 1988 to 1991. Prey provided for the 1st instar were spring-tail (*Sinella cuspidatus*) nymphs and adults and fruit fly (*Drosophila melanogaster*) adults. In the period after the 1st instar, prey were nymphs and adults of pill-bug (*Armadillium vulgare*), woodlice (*Porcellionides pruinosus*), and grasshopper (*Euparatettex histricus*). When these prey were not available, another grasshopper (*Oxya japonica* or *Atractomorha bedeli*) was at times used. These prey were selected according to the suitability of their body size for the experimental animals at different developmental stages, and were provided in rotation. The occurrence of molts was easily detected in the rearing container, since this spider ejects exuvium or its broken pieces from the web. Web width was measured 2–5 cm above soil level with a pair of slide callipers, and the measurement was repeated 3–5 times per year at arbitrary intervals.

Observation on excretion activity. Since this spider ejects excreta from the top of the web, the excreta always sticks to the inside of the container. When the inside of the container is cleaned regularly, the number of times the spider has excreted since the last cleaning of the container can be counted. In order to investigate the seasonal change of excretion frequency as an index of vital activity, the number of times per week that each of six 4th–6th instar nymphs and 5 adult females excreted was counted throughout 1989. These 11 spiders were collected in the field on 29 November 1988. After an accommodation period of 32 days, observation was started on 1 January 1989. Rearing methods were the same as in the individual rearings described above.

Collection of specimens in the field. Many adults and nymphs of different instars were collected at haphazard on 16 October 1986 and 27 April 1987 for examining the relationship between body size and web size. Before digging out webs from the ground, the width and height of each web were measured. The total number of specimens obtained was 57, of which 12 were adult females and 2 males. These specimens were killed at once and preserved in 80% alcohol for measuring the width of the sternum and carapace. Measurement was made under a binocular microscope equipped with a micrometer scale. However, the 2 adult

males were not examined because the number was too small to establish the relationship between body size and web size. In order to assess the relationship between the adult female's body size and the number of nymphs produced, large webs were selectively dug out in the field on 12–13 November 1988 and 21–22 November 1989, and 49 females with their nymphs were obtained. The females were preserved in 80% alcohol for measuring, and the number of nymphs present in the webs was counted. For the purpose of estimating the mating season, large webs were also dug out on 4 occasions at intervals of 12–15 days during June and July 1990. Eighteen mating pairs were found in the females' webs, and were preserved in 80% alcohol for measurement.

Results and Discussion

Development of nymphs and web growth. Figure 1 shows the occurrence of molts during the development of 1st instar nymphs under semi-outdoor conditions. As described elsewhere in detail, this spider has distinct postembryonic developmental stages, larva and prenymph, before emergence to 1st instar nymphs (YOSHIKURA, 1958). Therefore, 1st instar in this paper means the stage at which nymphs first begin their independent life after dispersal from the mother's web.

Mortality during the course of rearing was quite high, especially in the first winter; *i.e.*, total mortality was 78.8% of which 61.0% occurred in the first winter. After the first winter, the mortality reduced greatly.

As shown in the graph, 4 males and 7 females were successfully reared to

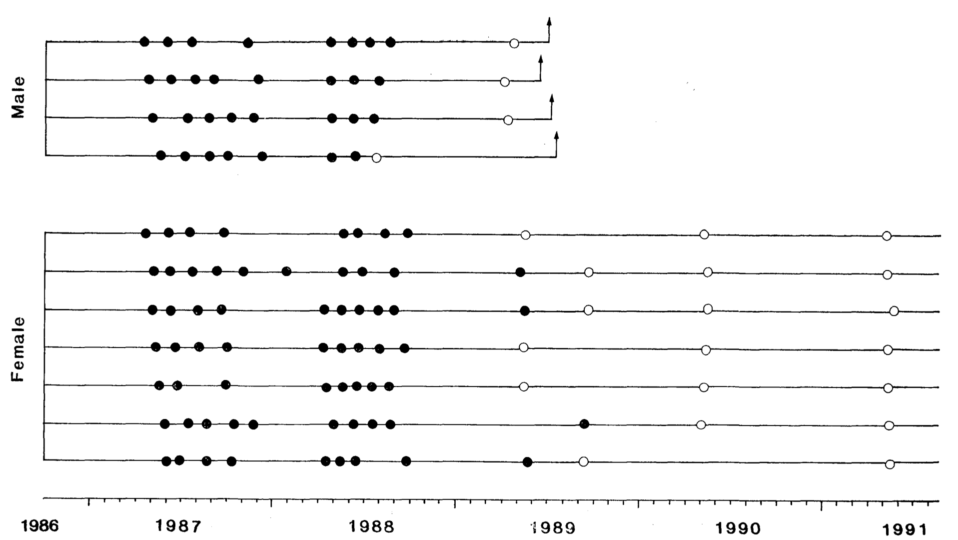

Fig. 1. Course of development of males and females under semi-outdoor conditions. Solid circles indicate ordinary molts, open circles represent the adult and succeeding post-adult molts. Arrows show emergence from web.

adulthood. Males required 3 years for development, passing through 8–9 molts. Molts generally occurred during the period from late May to October and/or November, and not during winter. The males emerged from their webs to search for mates in June–July of 1989 and walked about within the rearing containers until they died at the end of August.

In the case of females, 6 individuals among 7 also required 3 years for development; *i.e.*, 3 emerged as adults in May and the other 3 in September. Those females which emerged in September may participate reproduction in the next year, since the main mating season is June–July. The rest one emerged in May 4 years after their birth. The number of molts ranged from 9 to 11. Molts occurred during the same period as for males. In addition, a post-adult molt was repeated once a year throughout the survival period. This post-adult molt generally occurred in April–May every year. Post-adult molting is common for female mygalomorph spiders. STRADLING (1978) studied in detail the growth and maturation of *Avicularia avicularia* L. by measurement of exuviae, and ascertained the occurrence of successive post-adult molts at intervals of about one year. A similar post-adult molt is also known to occur in some Liphistiidae, for example *Heptathela kimurai* (KISHIDA) (YOSHIKURA, 1987). AOKI (1983) investigated the life cycle of *A. karschi* by measurement of carapace width of the spiders sampled monthly in the field, and described that new-born nymphs

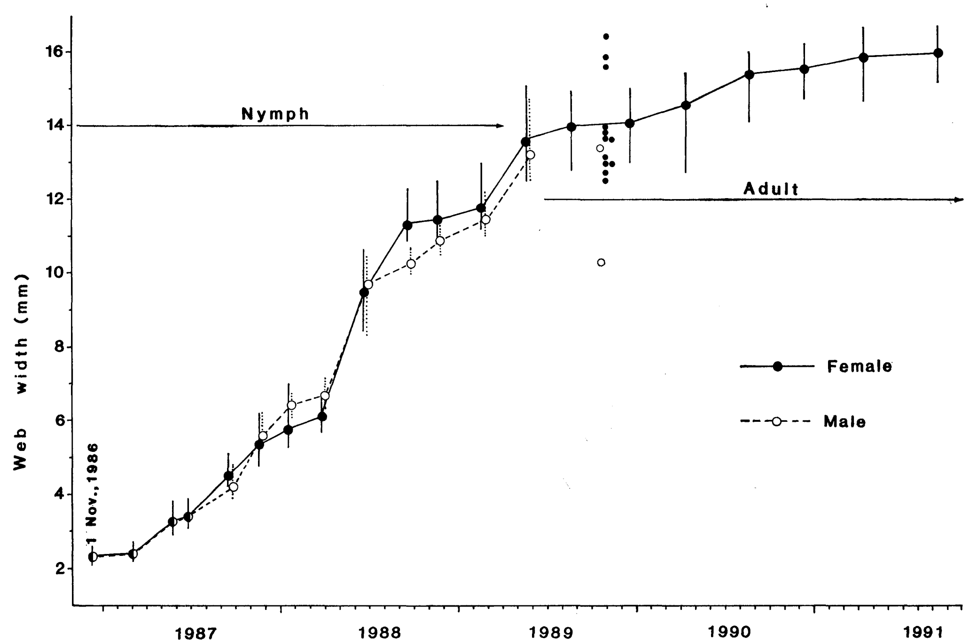

Fig. 2. Growth of web width during nymphal and adult periods under semi-outdoor conditions. Large open and solid circles indicate mean widths for males and females respectively; the vertical dotted and solid lines show the range. Small open and soild circles show the web widths for males and females colletced in the field.

matured at 5th instar in 3rd year from their birth. However, his description is somewhat inaccurate in view of the rearing results described above, and he overlooked the occurrence of post-adult molts.

Experimental animals enlarged their webs by digging into the soil as development porceeded. By measuring web size from season to season, therefore, it is possible to trace the growth of the spiders. Direct measurement of body size was impossible, because experimental animals frequently failed to spin new webs in rearing containers after they had been dug out from the soil. Figure 2 shows the results of 5 years measurement of the web width of the individuals which successfully developed to adulthood. Web height was also extended as development proceeded, but it varied greatly even among nymphs of the same instar. Web width was more regularly enlarged in proportion to body size than web height. As shown in Fig. 3, there was a close relationship between web width and body size of spiders collected at different instars in the field. In addition, sternum width was correlated closely with carapace width; thus in this paper sternum width is used as the index of body size, because the sternum is an easily measurable flat srtucture as compared with carapace.

According to Fig. 2, new-born 1st instar nymphs showed no remarkable growth until spring of the next year. In the field, they usually overwinter together with their mother in the web. Feeding of the offspring by the mother during overwintering is, however, unknown. The nymphs commenced to enlarge the web rapidly after overwintering, and this pattern was maintained until their 3rd spring by which time most of them had developed to adulthood. The mean web widths increased from 2.3 mm to 13.3 mm (5.8 times) for males and 13.7 mm (5.9 times) for females during this period. There was thus no significant dif-

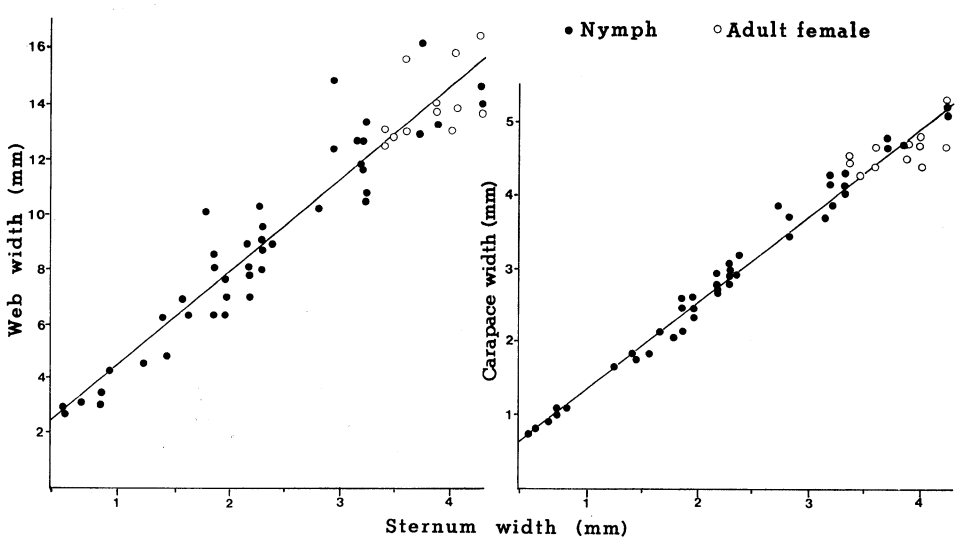

Fig. 3. Left: the relationship between sternum width and web width (regression line: $y=1.123+3.351x$, $r=0.950$, $P<0.01$). Right: the relationship between sternal width and carapace width (regression line: $y=0.223+1.163x$, $r=0.988$, $P<0.01$).

ference in the growth rate between males and females, although the former had somewhat smaller web widths than the latter ($P>0.05$ by t-test). In the case of females, growth continued during the following 2 years, and the mean web width reached 15.9 mm (6.9 times) by the autumn of 6th year. Thereafter, webs often began to show abnormal shape and structure; *i.e.*, they were bent around the brim of the container and thickened all over due to restriction imposed by container. Therefore, measurement of the web width was abandoned.

The small circles in Fig. 2 indicate the web width measured for adults collected in the field during October 1986 and April 1987. Comparing these circles with the growth curve of female web width, it appears that the adult female's web width was considerably smaller in the field than it was under our experimental rearing conditions. In fact, webs more than 16.0 mm in width were found only rarely in the field observation. This was probably due to the following 2 causes; 1) development of small-sized adults in the field due to the limited food supply, and 2) a high adult mortality rate in the field. There have been several reports of the appearance of small adults in relation to a poor food supply. TURNBULL (1962, 1965) reported that *Linyphia triangularis* CLERCK and *Agelenopsis potteri* (BLACKWALL) matured at smaller size when they were reared with a restricted food supply. VOLLRATH (1987) also presented a graph illustrating the same fact in *Nephila clavipes* (L.). SUZUKI and KIRITANI (1974) obtained small-sized adults of *Lycosa pseudoannulata* (BÖS. et STR.) when they were reared under poor food conditions, while MIYASHITA (1968) obtained larger adults of *Lycosa T-insignita* (BÖS. et STR.) when they were fed every 4th day than when they were fed every day, due to an increase in the number of molts. Heavy adult mortality would be effected to reduce the number of large adults.

Life cycle. According to the field observations, eggs were found in females' webs from July to early September. They were deposited in a thick sac attached tightly to the wall of web 3–4 cm above the bottom. However, YAGINUMA (1978) and AOKI (1983) reported that the oviposition period of this spider is generally from August to September. This disagreement in oviposition period suggests the existence of local difference in it. YOSHIKURA (1958) found that, after hatching from eggs in 12 days, hatchlings required a postembryonic developmental period of about 30 days including 2 molts; *i.e.*, 10 days as a larval stage and 21 days as a prenymphal stage. In the field, the emergence of 1st instar nymphs was considered to occur from late October to late November, since ejection of the nymphs' exuviae from the webs by mothers was most frequently observed in this season, although AOKI (1983) reported the emergence of 1st instar nymphs during September–October. The 1st instar nymphs remained in their mother's web until the spring of the following year. Webs in which nymphs remained together with their mother began to decrease gradually in number from mid March to April, and had finally disappeared by late April. It is considered, therefore, that the dispersal of nymphs from the mother's web occurs mainly from late March to mid April.

Very little is known about the ballooning behavior of this spider, although KATSURA (1975) reported one example observed in Shiga Prefecture on 7 April 1974. COYLE (1983) pointed out that ballooning occurs rarely in mygalomorph spiders as compared with araneomolph, and described in detail the manner of

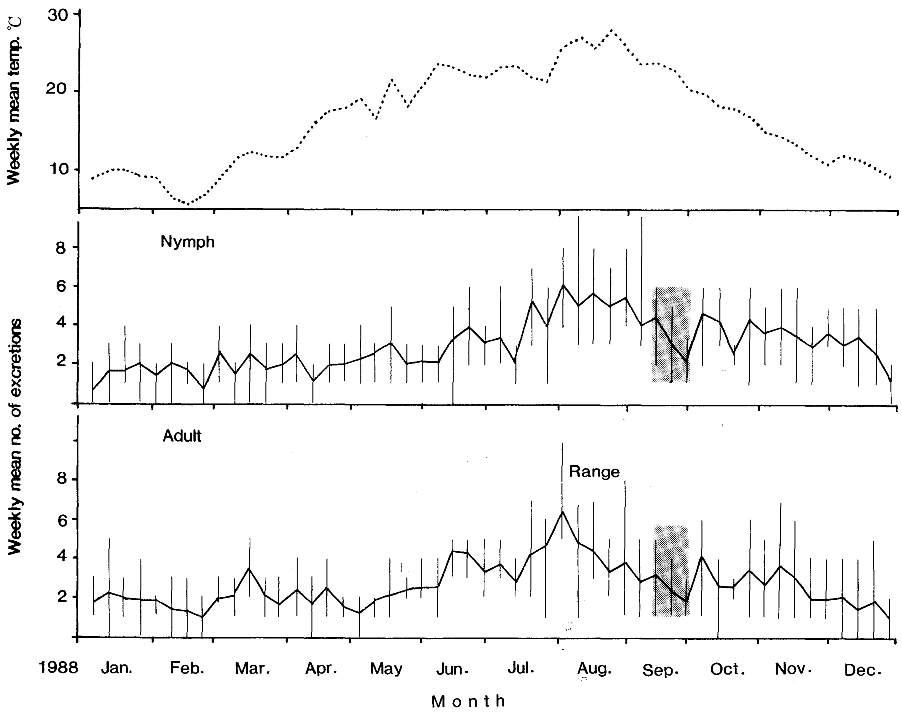

Fig. 4. Seasonal change in weekly mean number of excretions per individual for 6 nymphs and 5 adult females under experimental rearing conditions. Vertical lines indicate ranges, and the shaded area represents the period of food deprivation.

aerial dispersal by a mygalomorph spider, *Sphodros atlanticus* (GERTSCH et PLATNICK). According to COYLE *et al.* (1985), an important characteristic connecting with the rare occurrence of ballooning in mygalomorphs is a larger body mass of ballooning spiderlings as compared with that in araneomolphs.

New-born nymphs start their independent life during April–May. Their development and growth from that time on follow the course shown in Figs. 1 and 2. These graphs, however, indicate that an interruption of molting and a certain retardation of web growth were observed in winter. Whether this phenomenon is due to the existence of overwintering diapause was determined by looking for excretion activity. Figure 4 shows that excretion activity fluctuated in parallel with the seasonal change of weekly mean temperature without a definite cessation during winter. This indicates that the nymphs and adults of this spider do not enter into diapause in winter; rather they continue to feed and excrete throughout the year when prey are available. As shown by the shaded part of the graph, the number of times they excreted declined linerly when food was not provided. The decline of excretion activity during winter, therefore, may be a joint effect of low temperature and poor food condition.

New adult males emerge from April to May and go out from their webs for

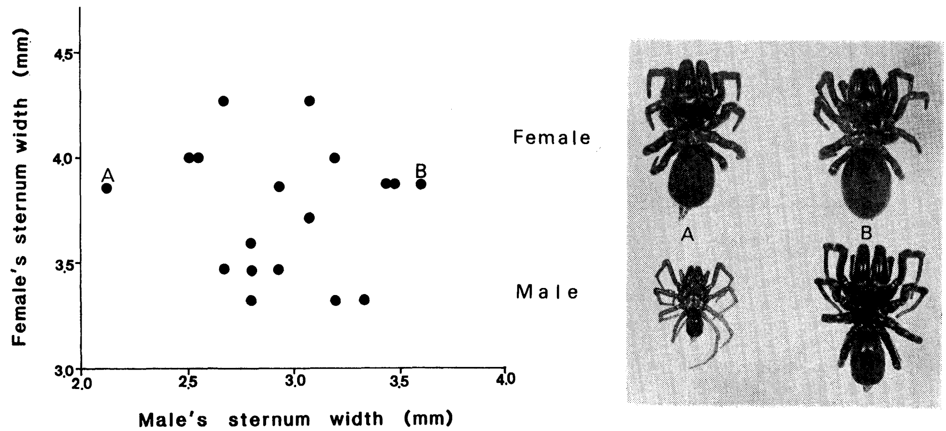

Fig. 5. Relationship between male and female sternal width in 18 pairs collected in the field, and a photograph showing the 2 pairs indicated by A and B in the graph.

searching mate in June–July. New adult females which completed their development by early June are ready to mate, but the other individuals emerged in August or thereafter overwinter and first mate in June–July of the next year. Old females more than one year finish their post-adult molt by June and are ready to mate. When we dug out large female's webs in June–July in the field, a male was sometimes found in them together with the resident female. The period during which such male and female pairs were most frequently found was from mid June to mid July. Therefore, the main mating season is from June to July, although AOKI (1983) had recognized the period from July to August as the mating season. In 1990, 18 pairs were obtained by seelctive digging of large webs in the field from early June to late July. Figure 5 shows the relationship of female to male body size as represented by sternum width for these 18 pairs. The right hand photograph is a comparison of 2 extreme pairs of medium-sized females mated with quite small (A) and large (B) males. It is clear from the graph that there was no relationship between the body sizes of successfully mated males and females. In the individual rearings referred to in the previous section, females never came out from their webs, whereas males came out during June–July and walked about in the container. In the field, therefore, males must visit females staying in their webs in the mating season, and females seems to accept any visiting males irrespective of their body sizes.

Figure 6 shows the relationship between female body size and the number of nymphs produced in 49 individuals collected in the field. The graph shows that larger females tended to produce more eggs, and mean number of nymphs produced per female was calculated to be 124.5 $\pm$ 63.6 (SD). Since the size of the sternum does not simply indicate the post-maturity age of that female, it is very difficult to judge whether or not the female's post-maturity age has a close connection with fertility.

Accurate longevity of adults is unknown. In the field, many adult females are suspected to die within 3–4 years because larger webs more than 16.0 mm

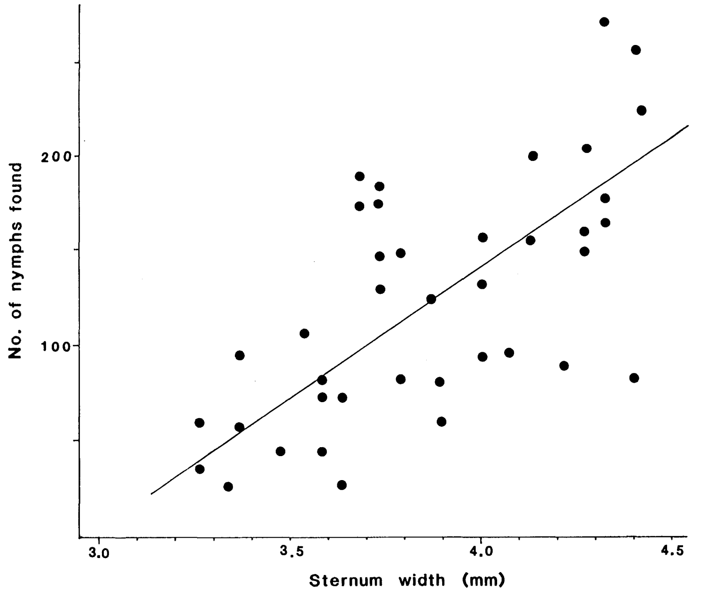

Fig. 6. Relationship between female sternal width and the number of nymphs produced (regression line: $y = 137.99x - 408.47$, $r = 0.757$, $P < 0.01$).

were rare in number, but a few seem to survive for 5–10 years because 3 adult females among 8 collected together with their offspring in autumn 1986 are still surviving under the conditions we used for individual rearings at the time of writing, 15 October 1992. In addition, these 8 females have never produced fertilized eggs in captivity. This means that yearly mating is necessary to produce fertilized eggs each year. If yearly mating was allowed, these females might be able to reproduce successfully for several years. No information on adult male longevity was obtained in this study.

摘　要

母グモの網より分散する少し前の幼生（若虫）を半自然条件下で個体飼育したところ，雄は8～9回脱皮をし，生まれてから3年目の春に成体になった．雌では，9～11回脱皮をして3年目の春と秋および4年目の春に成体になるものが生じた．飼育開始から3年目の春までの巣網の直径の成長を調べたところ，雄では2.3 mm より 13.3 mm に，雌では2.3 mm より 13.7 mm に成長した．雌の網の直径はこの後も成長をつづけ，5年目には15.9 mm に達した．また，雌は成体になってからも毎年春に1回脱皮を繰り返した．幼生と成体の1週間当りの排泄回数を1年間にわたって調べたところ，排泄回数は夏に増加し冬には減少したが，排泄が完全に停止してしまう訳ではなかった．これらの調査結果と，これらに平行して行なった野外調査の結果とを合わせ，このクモの生活環を考察した．

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